

## Developmental Mode in Opisthobranch Molluscs from the Tropical Eastern Pacific Ocean

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**Abstract.** Little has been published on mode of development in benthic opisthobranchs from the tropical eastern Pacific Ocean. Based on observations of uncleaved eggs, developing embryos, or hatching larvae, we determined or inferred mode of development for 43 species collected primarily from Bahía de Banderas, México. Forty-two of these, including the umbraculoidean *Tylodina fuugina*, had planktotrophic development, while *Phidiana lasercrucensis* hatched as lecithotrophic larvae. Both the sacoglossan *Elysia pusilla*, which had small eggs, relatively large egg capsules, and irregular strands of extra-capsular yolk in its egg mass, and the dendronotacean *Lomanotus vermiciformis* may also have lecithotrophic development in this region. Combined with previously existing data, mode of development is now known for 91 species of native, benthic, shallow-water opisthobranchs from the eastern Pacific and can be tentatively inferred for another 13 species based on data from other regions. Four species hatch as lecithotrophic larvae, and the remaining 100 as planktotrophic larvae. The prevalence of planktotrophic development in opisthobranchs from the eastern Pacific is similar to that known from the adjacent northeast Pacific Ocean, but is higher than in the less productive waters of the Caribbean Sea and the tropical western Atlantic Ocean, where opisthobranch eggs attain much larger diameters and 37% of the 112 species examined have either lecithotrophic or direct development. These results agree with those known for a diverse range of marine invertebrates across the Isthmus of Panama and are consistent with evolutionary trends expected in the egg size and mode of development with historical changes in ocean productivity and larval feeding environment.

### INTRODUCTION

More than 90% of 126 native species of opisthobranchs studied from the cool temperate waters of the northeast Pacific Ocean have planktotrophic development, a high prevalence thought to reflect the region's suitability for larval feeding and growth, especially its generally slow currents, large geographic expanse, and primary production driven by coastal upwelling and horizontal advection via the California Current, (Goddard, 2004). In contrast, relatively little information has been published on developmental mode in opisthobranchs from the tropical eastern Pacific (hereafter E Pacific), which includes the Panamic biogeographic province and extends from southern Baja California Sur to central Peru (Briggs, 1974). Here we document developmental mode in 43 species of shallow-water opisthobranchs known from the Pacific coast of Mexico, and compare the frequencies of the major modes of development to those known from the NE Pacific as well as the neighboring Caribbean Sea and

greater tropical western Atlantic Ocean (together referred to hereafter as the W Atlantic).

Based on the distributions reported recently by Behrens & Hermosillo (2005), Camacho et al. (2005) and Hermosillo et al. (2006), 17 species included in Goddard (2004) have ranges extending well into the Panamic province. Excepting *Antacolidiella indica* (Bergh 1888), which has lecithotrophic development and is circumtropical in distribution, all have planktotrophic larval development. Gonsalves-Jackson (2001, 2004) compared development in opisthobranchs across the Isthmus of Panama, and observed "planktonic" development in all 39 Pacific species she studied. Although Gonsalves-Jackson (2004) did not distinguish between planktotrophy and pelagic lecithotrophy, the small egg-sizes she reported (under 70 microns for sacoglossans and under 115 microns for all other species), combined with her descriptions and illustrations of embryos and hatching larvae, reliably indicate planktotrophic development for all 39 species, based on morphological criteria and known egg-size distribu-

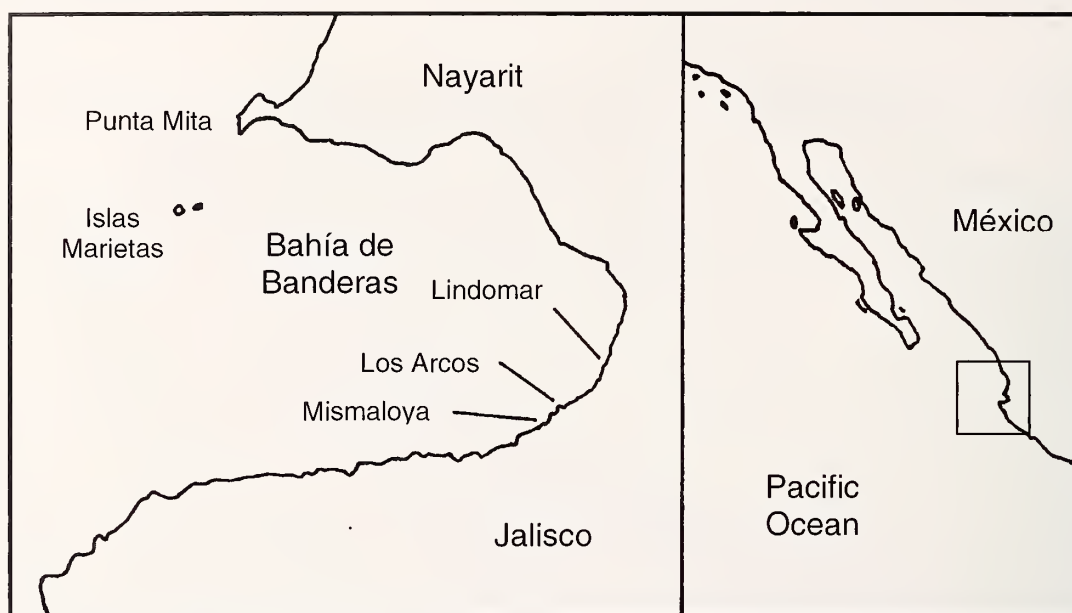


Figure 1. Map of Bahía de Banderas, México, showing collection localities.

tions (Thompson, 1976; Bonar, 1978; Hadfield & Miller, 1987; Goddard, 2004). Finally, information on the development of 13 of the more widely distributed Panamic opisthobranchs has been obtained from other regions of the world. Owing to the possibilities of geographic divergence and poecilogony, these latter data cannot be considered definitive for the E Pacific, but do suggest that *Lomanotus verniformis* Eliot 1908 and *Phestilla lugubris* (Bergh 1870) have lecithotrophic development, and that the remaining 11 species are planktotrophic (Harris, 1975; Bandel, 1976; Clark & Goetzfried, 1978; Switzer-Dunlap, 1978; Schmekel & Portmann, 1982; Gonsalves-Jackson, 2004; Table 1). Taken together, these data suggest that the prevalence of planktotrophy in the E Pacific is similarly high to that observed in the NE Pacific.

To better compare developmental mode in opisthobranchs from the two regions, we present here data on the development of 45 species of opisthobranchs from the Panamic biogeographic province. We then compare our results from the E Pacific to those from the more seasonally stable and relatively oligotrophic waters of W Atlantic, where a shift toward larger egg sizes and benthic or non-planktotrophic modes of development has been documented in opisthobranch gastropods (Gonsalves-Jackson, 2001, 2004), as well as other taxa, including bivalve molluscs, crustaceans, echinoid echinoderms, and bryozoans (Lessios, 1990; Jackson & Herrera, 1999; Marko & Moran, 2002; Wehrtmann & Albornoz, 2002; Fortunato, 2004; Moran, 2004).

During our survey, we were able observe the egg masses and hatching larvae of the umbraculoidean

opisthobranch *Tylodina fungina* Gabb, 1865. Because so little is known about the development and larvae of umbraculoideans (see Gibson, 2003), we also provide here a detailed description of its egg mass and hatching larvae.

## METHODS

Adult opisthobranchs and opisthobranch egg masses positively identified in the field were collected by hand from 16–28 February 2006 from subtidal and intertidal sites within Bahía de Banderas (20°30'N, 105°30'W), in the states of Jalisco and Nayarit, on the west coast of Mexico (Figure 1). This bay, approximately the size, shape and depth of Monterey Bay, California, and the collecting localities, have been described by Hermosillo (2003). Local sea surface temperatures during our work period averaged approximately 21°C. Adults were held in the field laboratory in containers (250 to 2000 ml) of seawater at 19–23°C until they laid egg masses. Recently laid egg masses were examined using a compound microscope equipped with an ocular micrometer. If first cleavage had not commenced, the diameters of a random sample of 10 zygotes were measured in each egg mass; otherwise, an upper limit on zygote size was estimated by measuring the dimensions of a few randomly selected embryos at or before the gastrula stage and (or) the minimum dimension of tightly fitting egg capsules containing embryos at or before the gastrula stage of development. After initial examination, each egg mass (or a portion of a large egg mass) was then isolated in a separate, labeled vial. The seawater in these vials was changed

daily, and the egg masses examined daily for hatching. Hatching larvae were then examined, measured and in some cases photographed. Developmental mode (planktotrophic, lecithotrophic and direct) and larval shell type (coiled type 1 and egg-shaped, inflated type 2) were assigned according to the egg size distributions and larval morphological criteria described by Thompson (1961, 1976), Bonar (1978), Clark & Jensen (1981), Hadfield & Switzer-Dunlap (1984), Hadfield & Miller (1987) and Goddard (2004). After obtaining the above egg masses, most of the adult specimens were relaxed in 7.5%  $\text{MgCl}_2$ , fixed in 70% ethanol, and deposited as voucher specimens in the California Academy of Sciences. Other adults were returned alive to the field. We used an underwater data logger (StowAway Tidbit, Onset Computer Corp.) to record temperature at 10 min. intervals in our holding containers.

We estimated egg size for *Polycera alabe* (COLLIER & FARMER 1964) and late embryo size for *Lomanotus vermiformis*, by placing a mm scale bar next to egg masses in the field and taking underwater digital images. Additional data, obtained by the senior author in central and southern California and Baja California, (1) supplement the data for three species we collected in Bahía de Banderas, and (2) are given for six additional species whose geographic ranges include the Panamic province.

To compare frequencies of development modes in the E Pacific to those in the NE Pacific and the W Atlantic, we assigned developmental mode (according to the criteria mentioned above) using published data on species from the E Pacific, and then combined these results with our own. We then calculated the frequencies of the different modes of development for (1) the NE Pacific based on Goddard (2004, 2005), and Krug et al. (2007); and (2) the W Atlantic based on data and determinations of developmental mode in Bandel (1976), Clark & Goetzfried (1978), Eyster (1980, 1981), Clark & Jensen (1981), DeFreese & Clark (1983), Carroll & Kempf (1990), Cronin et al. (1995), Ortea (2001), Gonsalves-Jackson (2004), and Pierce et al. (2006). For 17 species from the W Atlantic we assigned mode of development as either planktotrophic or direct based on close-up images of egg masses with either small or large eggs/embryos in Valdés et al. (2006); our determinations for six of these species were confirmed by information in the other references cited above for the W Atlantic, giving us confidence that our determinations for the other 11 species (for which no other information exists) were accurate. Ortea (2001) listed egg sizes for 11 Caribbean species of the nudibranch genus *Doto*, but provided no information on hatching stages or type of development. For six of these species we assigned developmental mode based on the egg-size distributions known for each mode, conservatively considering species with eggs less than

100  $\mu\text{m}$  in diameter as planktotrophic, species with eggs greater than 165  $\mu\text{m}$  diameter as lecithotrophic, and those with eggs greater than 220  $\mu\text{m}$  as direct developers. To avoid tabulating Atlantic species more than once, we used Valdés et al. (2006) and the Sea Slug Forum (<http://www.seaslugforum.net/>) to check for synonymies and recent taxonomic revisions.

We used JMP (version 7.0, SAS Institute, Inc.) to (1) conduct contingency analyses of the frequencies of planktotrophic vs. non-planktotrophic (lecithotrophic and direct) development by region, and (2) compare egg size distributions by region. For the latter we excluded egg size data obtained outside the regions of interest, but used all other determinations of egg size available from the above sources, even if mode of development is unknown. Owing to (1) the large number of species of opisthobranchs from the W Atlantic found to have non-planktotrophic development, and (2) the lack of detailed phylogenies for most opisthobranch taxa across the Isthmus of Panama, we limited the contingency analysis of developmental mode by E Pacific vs. W Atlantic Oceans to the numbers of families, rather than species, with planktotrophic vs. non-planktotrophic development. To reduce the influence of phylogenetic constraints unique to particular families, we further limited this analysis to families common to both oceans.

## RESULTS

We found 70 species of opisthobranchs in Bahía de Banderas and obtained data on the development of 39 of these. Combined with the data on six Panamic species obtained by the senior author outside of Bahía de Banderas, data on development were obtained for a total of 45 species (Table 1). Forty-two had planktotrophic development, and the aeolid nudibranch *Phidiana lasercensis* Bertsch & Ferreira 1974 had lecithotrophic development (Table 1). Although we obtained data on the egg and embryo size, respectively, of the sacoglossan *Elysia pusilla* (Bergh 1872) and dendronotacean nudibranch *Lomanotus vermiformis* (Table 1), we did not observe their hatching stages and were unable to determine with certainty their mode of development. The former had small eggs but had relatively voluminous egg capsules surrounded by irregular strands of extra-capsular yolk (ECY) (Figure 2). As shown by Clark & Jensen (1981), the presence of these traits can indicate lecithotrophic or even direct development in sacoglossans, despite otherwise small egg size. The embryos of *Lomanotus vermiformis* observed in the field were large enough (Table 1) that none of the three major modes of development can be ruled out based solely on known distributions of egg size and shell size at hatching (Hadfield and Miller, 1987; Goddard, 2004). Clark &



Table 1

Comparative data on embryonic development in opisthobranchs known from the tropical eastern Pacific Ocean. Each row of data was obtained from a single egg mass, either collected in the field or deposited in the laboratory, with a dash (—) representing no data collected. Unless specified otherwise, all localities are in Bahía de Banderas, Jalisco and Nayarit, Mexico (see Figure 1). Mode of development: P, planktotrophic; L, lecithotrophic. If hatching larvae were not observed, mode of development was inferred based on the egg size distributions reported by Hadfield and Miller (1987) for the major modes of development, and comparisons with congeners (see Goddard, 2004). Inferred modes of development are in parentheses. Values for egg diameter and shell length at hatching are means, plus or minus one standard deviation, with sample size in parentheses. In cases in which zygotes were not observed, an upper limit for egg size is given, based on measurements of early embryonic stages (16 cell through gastrula), which are typically a little longer in greatest dimension than the zygotes (personal observations; see Methods). Temperature was recorded only in the laboratory and is given only for egg masses held for most or all of the embryonic period; sea-surface temperatures at our study sites in Mexico in February 2006 were approximately 21°C.

Taxon	Egg diameter ( $\mu\text{m}$ )	# eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell type	Shell length at hatching ( $\mu\text{m}$ )	Eyespots at hatching	Mode of develop- ment	Locality
<b>Cephalaspidea</b>									
<i>Haminocera virescens</i> (Sowerby 1833)	—	1	—	—	1	144.1 $\pm$ 4.7 (5)	no	P	Santa Barbara, California
CASIZ 174985	—	1	—	—	1	100.9 $\pm$ 4.7 (5)	no	P	Punta Mita
<i>Haminocera ovalis</i> Pease 1868	<81	1	—	—	—	—	—	(P)	Punta Mita
<i>Navanax aenigmaticus</i> (Bergh 1893)	—	—	—	—	—	—	—	—	—
<b>Anaspidea</b>									
<i>Phyllaplysia padinae</i> Williams & Gosliner 1973	<100	1	—	—	—	—	—	—	Lindomar
CASIZ 174105	—	1	—	—	1	121.4 $\pm$ 3.4 (10)	no	P	Bahia de Los Angeles, Baja California
<b>Umbraculoidea</b>									
<i>Tylodina fungina</i> Gabb 1865	73 <sup>a</sup>	1	—	20–23	1	126.0 $\pm$ 3.7 (5)	no	P	Los Arcos, subtidal
CASIZ 174054 (egg mass)	—	—	—	—	—	—	—	—	—
<b>Sacoglossa</b>									
<i>Elysia diomedea</i> (Bergh 1894)	<65	1	—	—	1	128.4 $\pm$ 2.4 (10)	no	P	Punta Mita
<i>Elysia pusilla</i> Bergh 1872	—	—	—	—	—	—	—	(L?) <sup>b</sup>	Punta Mita
CASIZ 174092	<73	1	—	—	—	—	—	(P)	Los Arcos, intertidal
<i>Oxynoe patmanensis</i> Pilsbry & Olsson 1943	—	—	—	—	—	—	—	—	—
CASIZ 174085	—	—	—	—	1	96.4 $\pm$ 2.9 (2)	no	P	Los Arcos, intertidal
<i>Polybranchia viridis</i> (Deshayes 1857)	—	—	—	—	—	—	—	—	—
CASIZ 174098	—	—	—	—	—	—	—	—	—
<b>Nudipleura: Pleurobranchidae</b>									
<i>Berthellina ilisima</i> Marcus & Marcus 1967	—	6–9	—	—	1	144.5 $\pm$ 0.4 (2)	yes	P	Santa Barbara, California
<i>Pleurobranchus areolatus</i> (Mörch 1863)	—	—	—	—	1	121.4 $\pm$ 3.1 (10)	no	P	Los Arcos, intertidal
<b>Nudipleura: Doridina</b>									
<i>Conualevia alba</i> Collier & Farmer 1964	87.7 $\pm$ 1.4 (10)	1	15–16	16–19	1	150.7 $\pm$ 2.5 (10)	no	P	Monterey, California
CASIZ 174704	90.1 $\pm$ 1.0 (10)	1	—	—	—	—	—	—	—
<i>Dendrodoris funata</i> (Rüppell & Leuckart 1831)	—	1	—	—	—	151.2 $\pm$ 3.4 (10)	no	—	—
CASIZ 174096	101.6 $\pm$ 0.7 (5)	1	—	—	1	174.8 $\pm$ 4.8 (10)	no	P	Mismaloya



Table 1  
Continued.

Taxon	Egg diameter ( $\mu\text{m}$ )	# eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell type	Shell length at hatching ( $\mu\text{m}$ )	Eyespots at hatching	Mode of develop- ment	Locality
<i>Diaditula aurila</i> (Marcus & Marcus 1967) CASIZ 174061, 174101	87.9 $\pm$ 2.6 (10)	1–2	15	16–19	1	139.6 $\pm$ 5.7 (10)	no	P	Punta Rosarito, Baja California <sup>c</sup> Lindomar
<i>Doriopsisilla rovena</i> Marcus & Marcus 1967 CASIZ 174055	97.4 $\pm$ 3.1 (3)	1	—	—	—	—	—	(P)	Mismaloya
<i>Doris granulosa</i> (Pease 1860) CASIZ 174061	<73	1	—	—	—	—	—	(P)	Punta Mita
<i>Doris innumida</i> (Risbec 1928) CASIZ 174084	67.4 $\pm$ 1.2 (10)	1	—	—	—	—	—	(P)	Lindomar
<i>Jorinna</i> sp. 1 of Behrens & Hermosillo 2005 CASIZ 174099	<65	1	—	—	—	—	—	(P)	Punta Rosarito, Baja California
<i>Okenia angelensis</i> Lance 1966 CASIZ 174104	$\cong 62^d$	1	—	—	—	—	—	(P)	Mismaloya
<i>Okenia angelica</i> Gosliner & Berstch 2004 CASIZ 174093	<68	1	4	19–23	1	103.5 $\pm$ 1.9 (10)	no	P	Bahia de Banderas Marietas
<i>Polycera alabe</i> Collier & Farmer 1964 CASIZ 174087	$\cong 60^e$	1	—	—	—	—	—	(P)	Marietas
<i>Tumbija eliora</i> Marcus & Marcus 1967 CASIZ 174083	—	1	7	19–23	1	129.4 $\pm$ 2.5 (10)	no	P	Los Arcos, intertidal
<i>Thoridisa</i> sp. 1 of Behrens & Hermosillo 2005 CASIZ 173057	<80	1	5	19–23	1	120.5 $\pm$ 4.7 (5)	no	P	Mismaloya
<i>Tyrinna evelinae</i> (Marcus 1958) CASIZ 174083	<80 <81	1 1	6 —	19–23 19–23	1 1	127.4 $\pm$ 2.1 (10) $\geq 118^f$	no no	P P	
<b>Nudipleura: Dendronotina</b>									
<i>Doto</i> sp. 2 of Behrens & Hermosillo 2005 CASIZ 174090	<80	1	5	19–23	1	121.4 $\pm$ 4.6 (10)	no	P	Lindomar
<i>Doto</i> sp. 3 of Behrens & Hermosillo 2005 CASIZ 174089	<89	1	—	—	1	127.4 $\pm$ 8.8 (6)	no	P	Los Arcos, intertidal
<i>Doto</i> sp. (brown) CASIZ 174103	<80	1	—	—	1	104.3 $\pm$ 1.8 (2)	no	P	Montana de Oro State Park, California
<i>Haucockia californica</i> MacFarland 1923 CASIZ 174703	99.6 $\pm$ 2.1 (15)	1	10	12–17	2	242.9 $\pm$ 3.0 (20)	no	P	Bahia de Banderas Mismaloya
<i>Lomatitius verniformis</i> Eliot 1908 CASIZ 174703	—	—	—	—	—	$\cong 190^g$	no?	(L?) <sup>b</sup>	
<i>Lomatitius</i> sp. 2 of Behrens & Hermosillo 2005	65.0 $\pm$ 1.5 (5) 67.6 $\pm$ 2.0 (5)	1 1	5 —	19–23 —	1 —	— —	— —	(P) (P)	
<i>Tritonia pickensii</i> Marcus & Marcus 1967 CASIZ 174100	<69	1	—	—	—	116.8 $\pm$ 4.2 (10)	no	P	Lindomar
<b>Nudipleura: Acolidiina</b>									
<i>Acolidiella alba</i> (Risbec 1928) CASIZ 174100	69.7 $\pm$ 0.4 (10)	1	—	—	—	—	—	(P)	Mismaloya
<i>Acolidiella chronosoma</i> (Cockerell & Eliot 1905)	<85 <90	— 1	— 6.5	— 16–19	— 1	— 127.0 $\pm$ 4.3 (10)	— no	(P) P	Los Arcos, intertidal Punta Rosarito, Baja California <sup>c</sup> Lindomar
<i>CASIZ 174060, 174106</i> <i>Bajaolis bertschi</i> Gosliner & Behrens 1986 CASIZ 174097	<89	1	—	—	—	—	—	(P)	

Table 1  
Continued.

Taxon	Egg diameter ( $\mu\text{m}$ )	# eggs per capsule	Embryonic period (days)	Temp. (°C)	Shell type	Shell length at hatching ( $\mu\text{m}$ )	Eyespots at hatching	Mode of develop- ment	Locality
<i>Cuthonia lizae</i> Angulo & Valdés 2003	—	1	3.5	19–23	2	241.0 $\pm$ 6.0 (5)	yes	P	Mismaloya
CASIZ 173058, 174058	88.6 $\pm$ 1.4 (10)	1	—	—	—	—	—	(P)	Los Arcos, intertidal
<i>Eubranchius cucullus</i> Behrens 1985	<100	1	—	—	—	—	—	—	Lindomar
CASIZ 173062	—	—	—	—	—	—	—	—	—
<i>Eubranchius</i> sp. 2 of Camaeño-García et al. 2005	—	1	—	—	2	227.8 $\pm$ 3.2 (10)	yes	P	Los Arcos, intertidal
CASIZ 174057	—	—	—	—	—	—	—	—	—
<i>Eubranchius</i> sp.	<94	1	4	19–23	2	212.2 $\pm$ 3.2 (5)	yes	P	Los Arcos, intertidal
CASIZ 174094	—	1	—	—	2	203.2 $\pm$ 8.5 (5)	yes	—	—
<i>Favorinus elendlexiae</i> García & Troneoso 2001	<80	1	4	19–23	1	115.0 $\pm$ 1.8 (10)	no	P	Marietas
CASIZ 174060	—	—	—	—	—	—	—	—	—
<i>Flabellina marcusorum</i> Gosliner & Kuzirian 1990	<73	1	—	—	—	—	—	(P)	Lindomar
<i>Flabellina telja</i> Marcus & Marcus 1967	66.1 $\pm$ 0.6 (4)	1	4	19–23	1	123.7 $\pm$ 3.7 (10)	no	P	Mismaloya
CASIZ 174059	—	—	—	—	—	—	—	—	—
<i>Flabellina</i> sp. 1 of Behrens & Hermosillo 2005	<74	1	5	19–23	1	99.6 $\pm$ 4.9 (5)	no	P	Los Arcos, subtidal
CASIZ 173059	—	—	—	—	1	102.2 $\pm$ 1.8 (5)	no	—	—
<i>Hermosita lakuananata</i> Ortea, Caballer & Espinosa 2003	—	1	—	—	1	115.9 $\pm$ 5.6 (4)	no	P	Marietas
CASIZ 174088	—	—	—	—	—	—	—	—	—
<i>Phidiana lasrucensis</i> Bertsekh & Ferreira 1974	<150	1	—	—	—	—	—	—	Punta Mita
CASIZ 174056, 174102	146.6 $\pm$ 1.8 (10)	1	23	14–16	1	248.6 $\pm$ 7.2 (10)	yes	L	Bahía de Los Angeles, Baja California
<i>Spirilla neapolitana</i> (Delle Chiaje 1823)	<77	1–3	—	—	—	—	—	(P)	Lindomar

<sup>a</sup> Based on the diameter of two unclashed eggs in a field-collected egg mass containing embryos at the gastrula stage. Early embryos measured 73 to 85  $\mu\text{m}$  in longest dimension.

<sup>b</sup> Observations of hatching veligers are needed to confirm this mode of development (see text).

<sup>c</sup> Goddard (2004, unpublished data).

<sup>d</sup> Based on measurements of early embryos fixed in 70% ethanol.

<sup>e</sup> Estimate based on image of egg mass next to mm ruler taken in field (see Methods).

<sup>f</sup> Based on measurements of pre-hatching veligers.

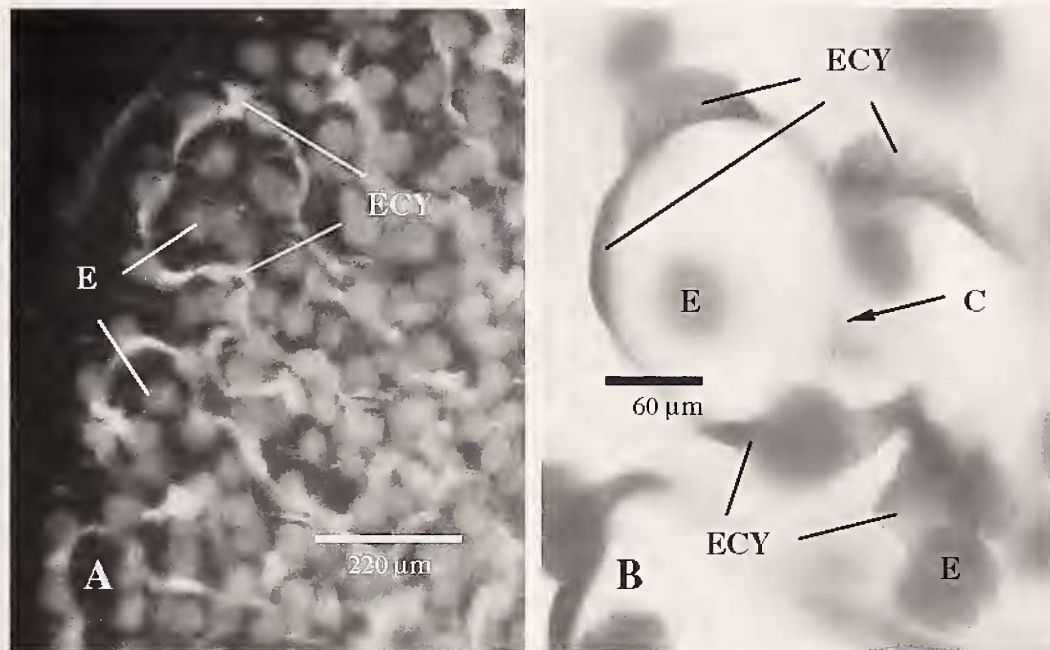


Figure 2. *Elysia pusilla*. A. Detail of egg mass, showing egg capsules (C), extra-capsular yolk (ECY), and embryos (E). B. Close-up of extra-capsular yolk on outside of egg capsules.

Goetzfried (1978) reported that this species has lecithotrophic development in Florida.

We obtained data on the development of nine undescribed species, eight of which are recognized and illustrated in Behrens & Hermosillo (2005), Camacho et al. (2005) or Hermosillo et al. (2006), and one of which (*Enbranchus* sp.) appears to be new. Our record of *Doris immonda* (Risbec 1928) from under coral rubble at Punta Mita, the northern boundary of Bahía de Banderas, is the first sighting of this species in Mexican waters and only the second record of its occurrence outside the Indo-west Pacific (Camacho et al., 2005). Voucher specimens for all ten of these species have been deposited in the California Academy of Sciences (Table 1).

Combined with previously existing data from the region (see Introduction), mode of development is now known for approximately 91 species of native, benthic, shallow-water opisthobranchs from the E Pacific and can be tentatively inferred for an additional 13 species based on published data from other regions. The aeolid nudibranchs *Antaeolidiella indica* and *Phidiana lasrucensis*, and likely also both the dendronotid *Lomanotus vermiformis* and the aeolid *Phestilla lugubris*, hatch as lecithotrophic larvae, and the remaining 100 as planktotrophic larvae (Table 2). Fifteen of the 39 E Pacific species studied by Gonsalves-Jackson (2004) were only identified to genus (with voucher specimens of each deposited in the American Museum of Natural History). Depending on the overlap with species we

studied, this might reduce the total number of E Pacific species whose development is known, but it wouldn't significantly affect the overall prevalence (approximately 4%) of lecithotrophic development known from this region. By number of species, the incidence of planktotrophic vs. non-planktotrophic development in the E Pacific did not differ significantly from that observed in the NE Pacific Ocean (Table 2, Likelihood ratio  $\chi^2 = 1.735$ ,  $P = 0.188$ ).

From the literature we were able to determine or infer mode of development for 112 species of opisthobranchs from the W Atlantic (Tables 2 & 3). Lecithotrophic and direct modes of development were more prevalent in the W Atlantic compared to the E Pacific, comprising 21% and 16%, respectively, of the 112 species. In the W Atlantic these non-planktotrophic or non-feeding modes of development occurred in 17 families (Table 3) from all of the major orders and suborders of benthic opisthobranchs, save the Umbraculida, the development of which has not been examined in the W Atlantic. Sixteen of these families have representatives in the E Pacific, where non-feeding development is known from four and planktotrophic development from all 16 (Table 3). Limiting the contingency analysis to these 16 families, the incidence of non-feeding development, by number of families, is significantly higher in the W Atlantic than in the E Pacific (Likelihood ratio  $\chi^2 = 5.830$ ,  $P = 0.016$ ).

The higher prevalence of non-planktotrophic modes of development in the W Atlantic Ocean, compared to



Table 2

Number of species of opisthobranch molluscs known or inferred to have planktotrophic, lecithotrophic or direct development in the tropical eastern Pacific Ocean, compared to the NE Pacific and tropical western Atlantic Oceans.

Region	Mode of development			Sources of data
	Planktotrophic	Lecithotrophic	Direct	
NE Pacific	116	4	6	Goddard (2004, 2005) Krug et al. (2007)
E tropical Pacific	100	4	0	Harris (1975), Bandel (1976), Clark & Goetzfried (1978), Switzer-Dunlap (1978), Schmekel & Portmann (1982), Gonsalves-Jackson (2004), Goddard (2004), present study
W tropical Atlantic	71	24	17	Bandel (1976), Clark & Goetzfried (1978), Eyster (1980, 1981), Clark & Jensen (1981), DeFreese & Clark (1983), Carroll & Kempf (1990), Ortea (2001), Gonsalves-Jackson (2004), Pierce et al. (2006), Valdés et al. 2006

Table 3

Number of species of opisthobranchs from the tropical eastern Pacific and tropical western Atlantic Oceans known or inferred to have planktotrophic or non-planktotrophic (= lecithotrophic and direct) development, by taxonomic family. Based on sources listed in Table 2; taxonomic classification according to Behrens & Hermosillo (2005) and Valdés et al. (2006). A blank space means that no representatives of that family are known from that ocean.

Family	Tropical eastern Pacific		Tropical western Atlantic	
	Planktotrophic	Non-planktotrophic	Planktotrophic	Non-planktotrophic
Aegiretidae	1	0	0	0
Aeolidiidae	6	1	3	2
Aglajidae	2	0	3	0
Aplustridae			2	0
Aplysiidae	10	0	7	1
Arminiidae	1	0	1	1
Boselliidae			1	0
Bullidae	0	0	1	0
Caliphyllidae	1	0	2	1
Chromodorididae	9	0	8	5
Conualevidae	1	0		
Corambidae	1	0	1	0
Cylichnidae	2	0	0	0
Dendrodorididae	3	0	2	4
Dorididae	18	0	8	4
Dotoidae	5	0	4	4
Eubranchidae	3	0	0	0
Facelinidae	5	1	3	3
Flabellinidae	4	0	1	0
Goniodorididae	2	0	3	0
Haminoeidae	2	0	3	1
Hancockiidae	2	0	0	0
Hermaeidae	0	0	2	0
Hexabranchidae			0	1
Limapontiidae	1	0	4	2
Lomanotidae	1	1	0	1
Oxynoidae	1	0	2	1
Placobranchidae	3	0	3	7
Pleurobranchidae	4	0	4	2
Polyceridae	4	0	2	0
Tergipedidae	2	1	0	1
Tritoniidae	3	0	1	0
Tylodinidae	1	0	0	0
Zephyrinidae	2	0	0	0
Total no. of species	100	4	71	41

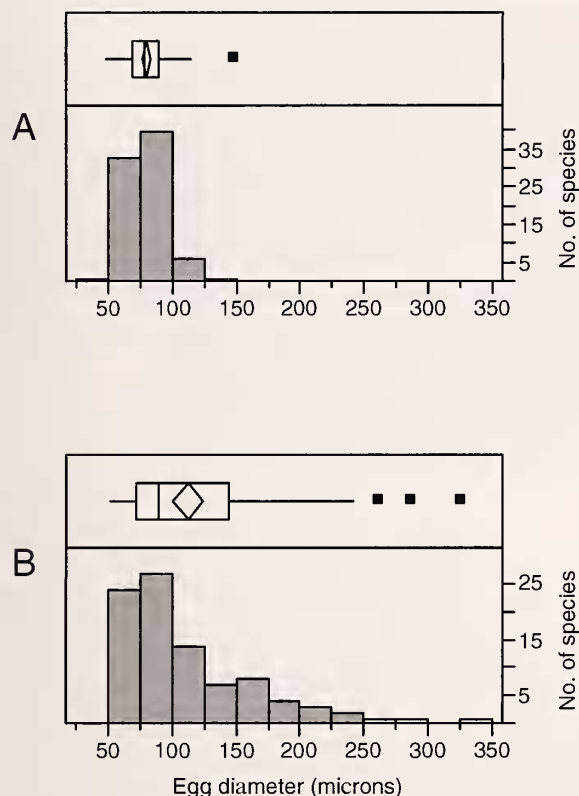


Figure 3. Egg size distributions, with box plots, for Opisthobranchia from the E Pacific ( $n = 81$  species) (A) and the W Atlantic ( $n = 92$  species) (B). The vertical line in the box plots indicates the sample median, and the diamond indicates the sample mean and 95% confidence intervals. The egg size distribution for the E Pacific is based in part on the upper size limits presented for some species in Table 1. The actual egg sizes for these species are slightly smaller (see heading for Table 1).

the E Pacific, is reflected in the strong skew toward larger egg sizes in the former (Figure 3).

## DISCUSSION

Planktotrophy is the dominant mode of development in opisthobranchs from the E Pacific, as in the NE Pacific. Differences in sea surface temperatures aside, both regions have productive waters seemingly conducive for larval feeding and growth. Seasonal, wind-induced, coastal upwelling and the slow-moving, nutrient-rich, California current fuel primary production in the NE Pacific (Bernal & McGowan, 1981; Chelton et al., 1982; Bakun, 1990; Mann & Lazier, 1991), while three types of upwelling (wind-induced coastal, equatorial, and that associated with the cyclonic gyre known as the Costa Rica dome) fuels production in the E Pacific (Wyrtki, 1964; McCreary et al., 1989; Mann & Lazier, 1991; Fielder, 1992). Larval food supplies in both regions are therefore probably rarely limiting, contrib-

uting to the evolutionary maintenance of small egg sizes and planktotrophy in taxa not historically constrained to non-feeding modes of development.

The lack of directly developing opisthobranchs in the E Pacific stands in contrast to the NE Pacific, where it has so far been documented in 6 species (Table 2). However, development has been examined in less than half of the total number of species of opisthobranchs known from the E Pacific (see Camacho et al., 2005; Hermosillo et al., 2006), and sampling in the E Pacific has been biased toward outer coast habitats and, in our study, the winter season. Additional sampling, including in estuarine habitats and during the summer (when a different complement of warmer water species may be present), may therefore be needed to determine if the observed difference in the frequency of this mode of development is significant. Although direct development is not yet known for any opisthobranch from the E Pacific, we suspect that *Chromodoris* sp. 1 of Hermosillo et al. (2006) may hatch as juveniles, based on its small adult size (10 mm) and a known geographic distribution limited to the Revillagigedo Islands, a small volcanic archipelago located 720 km west of mainland Mexico.

Eight of the species whose development we examined in this study were also identified and studied by Gonsalves-Jackson (2004) in Panama. In all cases our size measurements of eggs and embryos corresponded closely with her measurements of egg size, and our observations and measurements of hatching larvae were consistent with her sketches of embryos, only some of which depicted embryos near hatching (Gonsalves-Jackson did not provide measurements of shell size at hatching for any of the species she examined). The largest discrepancy in egg size was for the aeolid *Flabellina marcusorum*. Although we recorded its early embryos as being 73  $\mu\text{m}$  in largest diameter (indicating a slightly smaller egg diameter), and Gonsalves-Jackson (2004) reported a mean egg diameter of 81.5  $\mu\text{m}$ , this difference is within normal intra-specific variation, especially between different populations (e.g., Goddard, 1984, 2004; Todd et al., 2001).

Planktotrophy was significantly more prevalent in opisthobranchs from the E Pacific than in the W Atlantic, consistent with patterns in egg size and (or) mode of development documented by other workers for prosobranch gastropods, bivalve molluscs, alpheid crustaceans, bryozoans, echinoid echinoderms and reef-forming corals across the Isthmus of Panama (Lessios, 1990; Jackson & Herrera, 1999; Marko & Moran, 2002; Wehrtmann & Albornoz, 2002; Fortunato, 2004; Moran, 2004). Most of these studies intentionally compared life history traits in sister species thought to have diverged as a result of the rise of the Isthmus of Panama, thereby ruling out phylogenetic constraints as the sole determinant of the observed

geographic patterns in developmental mode. Larger egg-sizes and non-feeding modes of development are therefore thought to have evolved in these taxa as a result of environmental factors, namely the drop in productivity of surface waters in the Caribbean Sea and W Atlantic following the rise of the Isthmus of Panama (Bishop & Marra, 1984; Coates & Obando, 1996; Collins, 1996; Allmon, 2001). In this environment, larger eggs (with their greater yolk reserves) might be expected as one mechanism for offsetting the mortality caused directly or indirectly by lower ocean productivity and a poor larval feeding environment (e.g., Vance, 1973; Lessios, 1990). However, evidence presented by Moran (2004) for planktotrophic arcid bivalves, suggests that selection for reduced egg sizes in the E Pacific (in response to increased productivity following the rise of the Isthmus) may have been more important in shaping patterns of egg size across the Isthmus in that taxon. Moran (2004) also rightly notes that differential extinction of species with large eggs in the E Pacific and species with small eggs in the W Atlantic following the rise of the Isthmus might also be important in explaining recent egg size patterns.

Environmental considerations aside, phylogenetic constraints do not appear to be important in explaining the difference in mode of development observed in opisthobranchs across the Isthmus of Panama. Planktotrophy is known from nearly all of the 17 families with non-planktotrophic representatives in the W Atlantic and dominates the 16 of those same families that also occur in the E Pacific (Table 3). Given its widespread distribution among even higher taxonomic levels of opisthobranchs in the W Atlantic, non-planktotrophic development appears to have evolved independently in numerous lineages of opisthobranchs in this region.

The differences in ocean productivity and other environmental factors mentioned above apply on even broader geographic scales, and appear to be reflected in ocean basin-wide patterns of egg size and developmental mode in shallow water nudibranchs, the most species rich group of opisthobranchs (Goddard 1992, in preparation). In particular, data we have presented here support the hypothesis that eastern ocean regions, with their widespread upwelling, productive waters, and slow boundary currents (e.g., Mann & Lazier, 1991), will tend to maintain a higher frequency of planktotrophic development compared to western ocean regions, which have less productive waters at mid to lower latitudes and faster boundary currents, which might increase the risk of advection of larvae away from favorable settlement sites.

#### Notes on individual species

*Lomanotus* sp. 1 hatched as small, transparent, planktotrophic larvae with a coiled, type 1 shell

117  $\mu$ m long (Table 1). Because shell type is family-specific (Thompson, 1976; Goddard, 2004), the statement, without measurements, by Clark & Goetzfried (1976) that *L. vermiformis* (as *L. stauberi*) has an inflated, type 2 shell requires confirmation, especially given conflicting reports of shell type in the family. Thompson (1961), relying on Pruvot-Fol's (1954, fig. 142g) illustration of a coiled larval shell of *L. genei* Vérany 1846 from Europe, listed this species as having a type 1 shell. However, Thompson & Brown (1984) characterized the family Lomanotidae as having a type 2 shell, presumably based on Clark & Goetzfried's (1976) report for *L. vermiformis*.

#### *Tylodina fungina* Gabb 1865

The egg ribbons of *Tylodina fungina* were observed on the surface of its yellow, keratose sponge prey, identified in Bakus & Abbott (1980) as *Aplysina fistularis* (Pallas 1766) (= *Verongia thiona* de Laubenfels 1930). The egg masses were laid flat, often in overlapping, convoluted layers attached primarily to spongin fibers exposed by the grazing activity of adults (Figure 4A & B). The egg ribbons were similar in appearance to those of *T. perversa* (Gmelin 1791) and *T. corticalis* Tate 1889 known from E Australia and the Mediterranean Sea, respectively (Thompson, 1970; image in Poddubetskaia, 2002). The ribbons, though thin, were stiffer than those of most other opisthobranchs (personal observations), and appeared to be reinforced by transverse internal walls (Figure 4B). Egg masses laid on the sponge accumulated minute, golden brown, refractile bodies 1 to 5  $\mu$ m in greatest dimension (Figure 4C & D, compare to 4B). These bodies were likely unicellular cyanobacteria known to be associated with the surface layers of species of *Aplysina* (Maldonado & Young, 1998; Friedrich et al., 1999; Becerro et al., 2003; Usher et al., 2004). They did not occur inside the egg capsules of *T. fungina*, and appeared to accumulate in surface folds and furrows (Figure 4C & D). The refractile bodies gave the egg masses an opaque, pale yellow to pale orange-brown appearance and were often dense enough to obscure views of the embryos. In 70% ethanol the egg masses, like the adult slugs, turned deep purple, indicating the presence of uranidine, a pigment sequestered by species of *Tylodina* from their sponge prey (Teeyapant et al., 1993).

Near hatching, the embryos fit very tightly within their egg capsules, and the egg masses did not appear to break down as quickly as observed in more gelatinous opisthobranch egg masses. Hatching larvae lacked both eyespots and propodium, but had a compact, lipid-rich viscera, a distinctive, burgundy-colored mantle organ, and an operculum (Figure 4E). Their type 1 shells averaged 126  $\mu$ m in length (Table 1) and consisted of



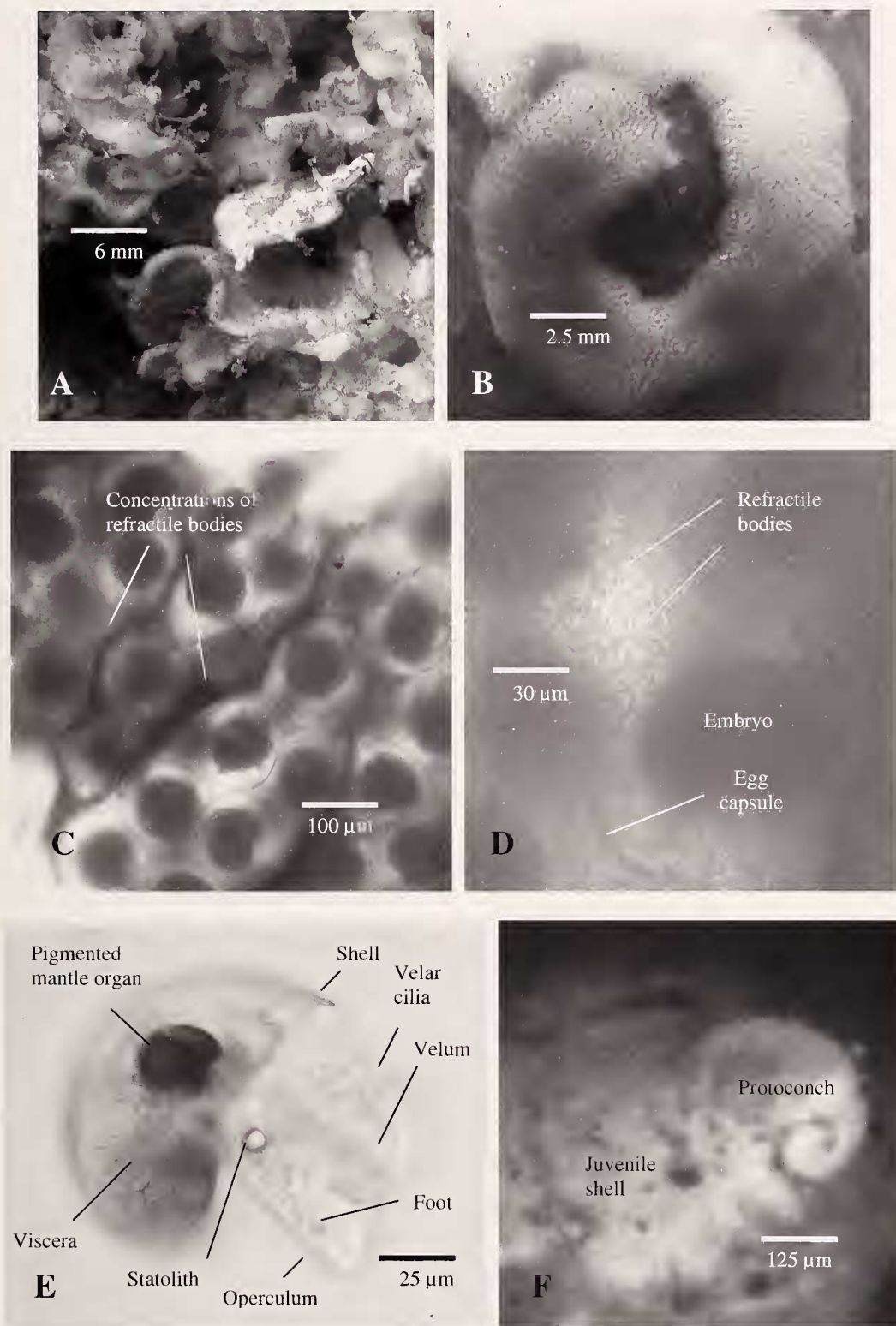


Figure 4. *Tyloedina fungina*. A. Egg ribbons laid on spongin fibers and remains of prey sponge, *Aplysina fistularis*. B. Egg ribbon laid on the dorsal surface of the shell of another *Tyloedina fungina*. Note the relative transparency of this ribbon compared to those laid on *A. fistularis*. C. Piece of egg mass removed from its sponge substratum, showing concentrations of minute refractile bodies on surface. D. Higher magnification view of minute refractile bodies on surface of egg mass. E. Newly hatched veliger larva, right lateral view. F. Apex of an adult shell (21.3 mm long), showing the protoconch (= embryonic and larval shell), left lateral view, and juvenile shell. Specimen from Bird Rock, La Jolla, California, 12 December 2004.

about two-thirds of a whorl. As observed in pleurobranchs, but not most other hatching planktotrophic opisthobranchs (Gibson, 2003), the mantle was not folded over the edge of the shell. We did not observe vigorous swimming by the newly hatched larvae.

The protoconch of an adult *Tylodina fungina* collected by the senior author at La Jolla, California measured 352  $\mu\text{m}$  in length and consisted of about 1.5 whorls (Figure 4F), indicating that the larvae of this species grow significantly in the plankton. Erosion of the outer layer of the protoconch was evident, but there did not appear to be any demarcation between the embryonic and larval shell (Figure 4F).

*Umbraculum umbraculum* (Lightfoot 1786) is the only other umbraculoid opisthobranch whose hatching larvae have been described. Like *Tylodina fungina*, the larvae of this species also hatch with coiled shell, a pigmented mantle organ, and an operculum (Ostergaard, 1950; Hartley, 1964). The egg masses, embryo size, and protoconch of *T. perversa* from the Mediterranean Sea appear very similar to those of *T. fungina* (Valdés & Lozouet, 2000; Poddubetskaia, 2002). *Tylodina corticalis* from eastern Australia lays egg masses similar to those laid by *T. fungina*, but with eggs 98  $\mu\text{m}$  in diameter (Thompson, 1970) may have lecithotrophic development.

The small size of the hatching larvae, their lack of both eyespots and propodium, and the size of the protoconch on the adult shell, all indicate that the larvae of *Tylodina fungina* are planktotrophic. However, the viscera developed in a compact arrangement reminiscent of lecithotrophic larvae, and the newly hatched larvae did not appear to be strong swimmers. It would be interesting to know if recently hatched larvae remain in the vicinity of the parental egg masses and consume the microbes associated with the egg masses and underlying sponge. Variation in such behavior might explain the affinity of some adult *Tylodina* for cyanobacteria associated with *Aplysina* (Becerro et al., 2003).

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